Within-season increase in parental investment in a long-lived bird species: investment shifts to maximize successful reproduction?

Schneider, N A ; Griesser, M

DOI: https://doi.org/10.1111/jeb.12561

Within-season increase in parental investment in a long-lived bird species: investment shifts to maximise successful reproduction?

Running title: within-season investment in long-lived bird

Nicole A. Schneider [1,2] and Michael Griesser [1,3,*]

[1] Department of Ecology, Swedish University of Agricultural Sciences, PO Box 7044, 75007 Uppsala, Sweden

[2] School of Zoology, Private Bag 5, University of Tasmania, Hobart 7001, Tasmania, Australia

[3] Anthropological Institute and Museum, University Zürich, 8057 Zürich, Switzerland

* Corresponding Author – Contact: michael.griesser@uzh.ch

Abstract

In nest-building species predation of nest contents is a main cause of reproductive failure and parents have to trade off reproductive investment against antipredatory behaviours. While this trade-off is modified by lifespan (short-lived species prioritise current reproduction, long-lived species prioritise future reproduction), it may vary within a breeding season, but this idea has only been tested in short-lived species. Yet, life-history theory does not make any prediction how long-lived species should trade-off current against future reproductive investment within a season. Here, we investigated this trade-off through predator-exposure experiments in a long-lived bird species, the brown thornbill. We exposed breeding pairs that had no prior within-season reproductive success to the models of a nest predator and a predator of adults during their first or second breeding attempt. Overall, parents reduced their feeding rate in presence of a predator, but parents feeding second broods were more risk sensitive and almost ceased feeding when exposed to both types of predators. However, during second breeding attempts, parents had larger clutches and a higher feeding rate in absence of predators than during first breeding attempts, and approached both types of predators closer when mobbing. Our results suggest that the trade-off between reproductive investment and risk-taking can change in a long-lived species within a breeding season depending on both prior nest predation and renesting opportunities. These patterns correspond to those in short-lived species, raising the question of whether a within-season shift in reproductive investment trade-offs is independent of lifespan.

Key words

Acanthiza pusilla, parental investment, predation, longevity, reproductive trade-off, feeding visits, approach distance, mobbing calls, prior experience, renesting opportunities

Introduction

In many nest-building species predation of nest contents is a main cause of reproductive failure (Ricklefs, 1969, Roff, 1992), exerting a strong selection on reproductive traits and driving individual adaptations that reduce predation risk (Fontaine & Martin, 2006, Lima & Dill, 1990). While much research has focused on parental adaptations that minimize nest predation risk (Martin & Briskie, 2009), predators can not only endanger their reproductive investment but also the survival of the parents (Lima, 2009, Ghalambor & Martin, 2001). Thus, predation will select for parental investment and antipredation strategies that increase the chance of successfully producing offspring without compromising parental survival.

Parents show a range of behavioural adaptations to reduce nest predation rates, such as avoiding breeding in locations where nest predators are abundant (Emmering & Schmidt, 2011), or minimising movements to and from the nest in the presence of nest predators (Eggers et al., 2008). However, the way how parents modify their antipredation behaviour depends on both who is at risk (nestlings or parents) and the life-history strategy of a species (Ghalambor & Martin, 2001). In long-lived species, parents are more sensitive to factors that reduce their own lifespan even at a cost to their offspring, whereas the opposite pattern is found in short-lived species (Ghalambor & Martin, 2001, Ghalambor & Martin, 2002). Even though life-history theory (Stearns, 1992, Charlesworth, 1980) makes clear predictions how parental investment varies across species depending on their lifespan, and empirical studies confirmed these predictions (Ghalambor & Martin, 2001), it remains unclear how parental investment changes within species across repeated nesting attempts within a breeding season.

Parental investment may increase during the breeding season due to declining within-season renesting opportunities (Andersson et al., 1980). This is supported by studies on multi-brooded bird species, showing that parents invest more into second than into first broods (Grüebler & Naef-Daenzer, 2008, Verhulst et al., 1997). In contrast, Brewer's sparrows *Spizella breweri* show a decrease in parental investment for repeated within-season breeding attempts (Chalfoun & Martin,

64 2010). However, these studies were done on short-lived species and thus it remains unclear if changes in reproductive investment within a breeding season depend on lifespan or is a consequence
66 of limited future breeding attempts. Independently of a species' life-history strategy, experience of prior nest predation may influence parental investment, as individuals can refine the probability of
68 losing their brood (called Bayesian updating; Valone, 2006). As a consequence, breeding individuals will increase their risk sensitivity (i.e. showing a stronger reaction in response to predators) and can
70 decrease their reproductive investment under high predation prospects (Schmidt & Whelan, 2010).

In this study, we investigate how parental investment and risk taking changes over a
72 breeding season in a long-lived bird species depending on who is at risk (parents or nestlings). Our setup allows us to investigate the investment trade-offs parents make between their own survival
74 versus the survival of their reproductive investment. As a study system we use brown thornbills (*Acanthiza pusilla*), a passerine species that faces high levels of nest predation (Higgins & Peter,
76 2002). The life-history traits of brown thornbills are characteristic of southern hemisphere bird species, with high adult survival, small clutch sizes, prolonged breeding seasons, repeated renesting
78 after nest failure, and prolonged post-fledging care (Green & Cockburn, 1999, Russell, 2000, Schneider & Griesser, 2013).

80 We exposed breeding pairs that had no prior within-season reproductive success (first nesting attempt of this season, or second nesting attempt where the first brood was depredated) to
82 models of a brood predator and a predator of adults. We aimed testing the following two hypotheses: (i) Parental investment and risk-taking may be threat dependent, such that parents
84 prioritise their own survival and take fewer risks in the presence of a predator of adults, as compared to a brood predator (Ghalambor & Martin, 2001). (ii) Parental antipredator investment may depend
86 on previous within season nesting success (Fig. 1). If parents use Bayesian updating and base their investment decisions on prior within-season nest predation experience, second broods will have a
88 lower expected survival value and thus receive less investment compared to first broods (Fig. 1, scenario i). However, if within-season renesting opportunities influence parental investment, the

investment should either not change since long-lived species show in general constant, low investment (Martin, 2004) (Fig. 1, scenario ii), or increase for consecutive breeding attempts as it will be the last chance of successfully reproducing within this season (Fig. 1, scenario iii).

Material and Methods

Study species and study site

Brown thornbills are small (6-9 g), long-lived (max. 17 yrs.) passerines endemic to the forests of south-eastern Australia that occupy small year-round territories (0.4-3.1 ha) (Green & Cockburn, 1999, Higgins & Peter, 2002). Thornbills typically nest in dense vegetation, with only females building the closed dome-nest and incubating the eggs, whereas males contribute to territory defence and to the rearing of nestlings and fledglings (Green & Cockburn, 1999). The clutch size is typically 3 eggs (range 2-4) and incubation takes about 18 days. Nestlings remain in the nest for about 16 days and depend on parental care for about 6 weeks after fledging (Green & Cockburn, 1999, Green & Cockburn, 2001). Nest predation is widespread (overall nest failure rate 62%; Green & Cockburn, 1999), occurring both during the incubation and nestling stage, and is mainly caused by avian predators (42%) and to a lesser extent by snakes (9%) or mammals (4%), or nests failed for other reasons (2%) (Green & Cockburn, 1999). Brown thornbills repeatedly renest after a nest failure and can, if successful, raise two broods per breeding season (Green & Cockburn, 1999). A rare reason for brood failure is the death of a breeder, which Green and Cockburn (1999) observed in 5% of all breeding events.

We studied brown thornbills within a 250 ha area of Trevallyn Nature Recreation Area (41°26’ S, 147°05’ E) close to Launceston, Tasmania, Australia. Brown thornbills are abundant at the study site and territories are densely spaced (64±6 territories per 100 ha). The vegetation at the study site consists of native eucalypt (*Eucalyptus* spp.) and wattle (*Acacia* spp.) woodland and an understory of large tussock grasses and bracken ferns. Between early October 2010 and early January 2011 we located brown thornbill nests and colour ringed the birds of 75 breeding pairs (for

116 details on used ringing technique see Griesser et al., 2012). Of the 85 nests we followed, 61 were located during the building, laying or egg stage, and 24 during the nestling stage. The number of
118 nests we used for our experiment was smaller (N = 21) because nests were predated before the experiment, either during incubation or during the nestling stage (N = 44). Moreover, some nests
120 were situated high up in trees (N = 4), or we experienced problems with the technical equipment during the experiment (N = 2) and thus excluded them from the analyses. Of the individuals included
122 in the experiment 83% were colour ringed.

We assessed the nesting attempt number of breeding pairs included in the experiment by (i)
124 monitoring pairs from the beginning of the breeding season (N = 15), or (ii) by setting a cut-off date (15^{th} November) for breeding pairs whose nests we found and monitored during a later stage of the
126 breeding season and where we did not observe fledglings on the territory (N = 6). By this date all breeding pairs in our population that we had followed since the start of the breeding season, and
128 that had lost their first brood through predation, had started their second breeding attempt (N = 17 out of all 85 nests). Each breeding pair was included only once in the experiment to avoid habituation
130 to the model species. The experiments were done under the license of the University of Tasmania Animal Ethics Committee (licence number A00110979).

132

Predator exposure experiment

134 We exposed 21 breeding pairs to perched models and calls of the main predator of adult birds (male collared sparrowhawk, *Accipiter cirrhocephalus*), the main brood predator (grey currawong, *Strepera*
136 *versicolor*), and a non-predatory species (dusky woodswallow, *Artamus cyanopterus*). Collared sparrowhawks are aerial ambush predators that hunt small birds and are a danger to adults and
138 fledglings of brown thornbill but not to nestlings (Marchant & Higgins, 1993, Barker & Vestjens, 1989). Grey currawongs forage in trees and on the ground by probing or gleaning and depredate
140 both eggs and nestlings of brown thornbill (Higgins et al., 2006, Barker & Vestjens, 1990). Dusky woodswallows are insectivorous passerines and pose no threat to adult thornbills, their eggs or

142 nestlings (Higgins & Peter, 2002). All these species breed at the study site (number of observed breeding pairs: collared sparrowhawk N = 1, grey currawong N = 6, dusky woodswallow N = 5).
144 Experiments were conducted when nestlings were around 10 days old (range 8-12 days) to reduce variations in parental investment in feeding and antipredator behaviours based on offspring age.
146 For each experiment, we positioned a digital video camera camouflaged with tree bark approximately 2 m from the nest, and filmed the nest entrance to get a clear view of parents
148 approaching the nest to feed the nestlings (brown thornbills are not disturbed by cameras close to their nest (Schneider & Griesser, 2013)). Each breeding pair received the following standardised
150 experimental treatment, with the presentation order of models being counter balanced between territories. First, in a 45 min pre-exposure period the nest was filmed without treatment as a
152 measure of baseline behaviour (i.e. feeding rate, food load size, number mobbing calls; see below). Thereafter, the experimenter positioned one of the models so that it was clearly visible at about 2 m
154 height and 8 m distance from the nest. Next to the model we placed an MP3 player connected to a speaker with built-in 2 Watt amplifier, and started playback with social territorial calls of the
156 respective model species (standardised playback volume, not louder than natural calls of the model species). The playback sequences consisted of 30 s of calls that were repeated every 5 min for the
158 total 45 min duration of the model exposure period. Playback sequences were unique for each model exposure and territory to avoid pseudoreplication (Kroodsma et al., 2001). This was done by using
160 recordings of the territorial calls for each species (using recordings of at least 5 individuals per species) and by randomly shuffling the sequence of call elements within and across the available
162 recordings (Schneider & Griesser, 2014). The experimenter always sat 10 m away from the nest, as the focal breeding pair was not disturbed by human presence at this distance (Schneider & Griesser,
164 2013). After the end of the model exposure period the experimenter removed the model and stopped the playback and the camera. Each breeding pair received a 30 min break before the next 45
166 min pre-exposure and model exposure period. The same set-up was repeated for the two remaining stimuli. All experiments were conducted in the morning by the same experimenter, with an entire

168 experimental block taking 5.5 h. In one experiment we were unable to finish the entire experimental block on the same morning and returned to the nest the following morning to finish the experiment.

170 In all experiments we assessed the minimum distance of either one of the breeding pair members to the models in the field as a measure of risk taking of the adult birds. During each 45 min

172 model exposure period and pre-exposure period of baseline behaviour, we manually counted the number of aggressive '*tzzt'* calls thornbills give when mobbing predators (Higgins & Peter, 2002)

174 using a combined count for male and female calls. In experiments where this could not be done with sufficient accuracy in the field due to a high calling rate, the number of calls was counted afterwards

176 from the video recordings (N = 8 experiments). As brown thornbills do not tolerate conspecifics pairs in their territory during breeding, even when encountering predators (Green et al., 2002; Schneider

178 personal observation, Green & Cockburn, 1999), the counted mobbing calls were most likely only from the experimental pair. From the videos we extracted the number of feeding visits (as a measure

180 of risk taking towards the brood), as well as the food load during the pre-exposure and model exposure periods. Food load size was estimated by the size of visible food items in the bills of parents

182 arriving at the nest. This was done by using bill length measures to calibrate the area of the digital video images (using ImageJ http://rsbweb.nih.gov/ij/) to calculate the area size of food loads

184 (following Martin et al., 2000).

186 ***Experimental groups selection & conditions***

To be able to compare changes in parental investment between breeding attempts within the same

188 breeding season we selected for our experiment pairs that had no prior within-season breeding success, i.e. pairs undertaking their first breeding attempt of the season (N = 8), and pairs

190 undertaking a second breeding attempt that had lost their first brood to predation (N = 13). This selection reduces potential biases in behavioural responses linked to previous within-season

192 breeding success.

Seasonal changes in food availability (e.g. insect abundance) may affect the workload of parents raising broods later on in the breeding season (e.g. Siikamäki, 1998, Low et al., 2010). However, insect availability most likely did not change during the study period. Canopy insect abundance in eastern Australian forests remains high throughout the breeding season given abundant spring and summer rainfall (Recher et al., 1996), which was the case in the year of our study (mean monthly rainfall Aug-Jan 1924-2013: 58.1 mm, mean monthly rainfall Aug 2010-Jan 2011: 68.3 mm) (Bureau of Meteorology, 2013).

Vegetation cover

Since the amount of cover at a nest site can modulate feeding rates when a predator is nearby (Eggers et al., 2008), we measured vegetation cover in the surroundings of all nests included into the experiment. Since all nests were located in the ground vegetation stratum (≤ 1 m height), we only assessed the ground vegetation cover. To assess the vegetation cover we vertically projected the crown and shoot area of all up to 1 m tall plants in a 5 m radius around the nest (small bushes, grass tussocks, ferns and herbaceous plants) to the ground surface, and estimated their amount of percentage cover (Mueller-Dombois & Ellenberg, 1974).

Statistical analyses

All statistics were performed using SAS 9.2 (SAS Institute, Cary, NC). We used Akaike's information criterion (AIC) as a method of finding the best-fitting model. AIC provides a measure of model fit accounting for the sample size and the number of parameters estimated in the model, with smaller values of AIC indicating a better-fitting model (Burnham & Anderson, 2002). We calculated AIC values corrected for small sample sizes AIC_C (Burnham & Anderson, 2002). From the initial, maximal model including all variables (see below) we constructed all possible candidate models. We calculated ΔAIC_C as the difference in AIC_C between a model and the best-fitting (final) model, which has ΔAIC_C of 0. The larger AIC_C is, the less plausible the fitted model is the best approximating model in the candidate

set. We also calculated AIC weights (ω_i) which give the likelihood that a model can be considered as the best model in the set of candidate models (Burnham & Anderson, 2002). We selected the final model as the model having the highest ω_i value and a minima $\Delta AIC_C = 2$ to the next candidate model. In the model output tables we present the best-fitting model.

For all response variables we constructed a maximal model that initially included all explanatory variables and all relevant two-way interactions (see below), with the number of nestlings and breeding pair fitted as random effects to control for eventual differences in parental feeding effort and exposing the same birds to all three model types. The two-way interactions included were those relevant for disentangling experimental effects, i.e. interactions between treatment (predator models vs. control), breeding attempt number, and exposure period (baseline behaviour vs. model exposure), as well as the interaction between treatment and ground vegetation cover (see model descriptions below for used variable combinations). Three-way interactions were not considered as small sample sizes can lead to a bias in these models and return confounding results (Quinn & Keough, 2002). In the final model, the effect of the different variables was clarified with the help of least square means (also called adjusted means).

Since parental investment could decrease in later breeding attempts due to declining offspring quality (Wallin, 1987), we ran a GLMM to test if offspring quality (measured as body mass/tarsal length, arcsine transformed) differed between first and second breeding attempts. As offspring quality did not differ between first and second attempts ($F_{1,12} = 1.14$, $p = 0.31$) we did not further consider it in the models. Moreover, parental feeding rate could be influenced by (i) parents compensating fewer feeding visits during predator exposure with increased food load sizes, and (ii) a seasonal change in insect food availability (Recher et al., 1996) and thus between consecutive breeding attempts. Therefore, we initially ran a GLMM (MIXED module, compound symmetric covariance structure) to clarify if parental food load size changed between baseline behaviour and model exposure. To test whether food loads, and thus indirectly food availability, changed between breeding attempts we ran a GLMM (GLIMMIX module) comparing parental food load size during

baseline behaviour for first and second breeding attempts. Since the residuals of the response
246 variable food load were non-normal distributed, we used a Lognormal distribution (identity-link), which provided a much better fit as indicated by the Pearson statistics (0.70). The Pearson statistics is
248 a reliable indicator for the fit between the chosen error distribution and the error distribution of the data where values of 1 represent a perfect fit (SAS, 2006). As food load neither changed between
250 model type and exposure period ($F_{2,46}$ = 0.28, p = 0.76), nor between breeding attempts over the season ($F_{1,392}$ = 1.54, p = 0.22), we did not include these variables into the models as it will not
252 confound our measure of parental feeding investment.

To analyse for changes in parental feeding investment between the pre-exposure period
254 (baseline behaviour) and the model exposure period we tested for the effect of treatment, breeding attempt number, and ground vegetation cover using a GLMM with a compound symmetric
256 covariance structure (MIXED module), comparing 40 different candidate models (see electronic appendix, Table 1). To investigate the risk to which parents expose themselves we tested how the
258 minimal parental approach distance to the presented model species was affected by the type of treatment, breeding attempt number, and the ground vegetation cover using GLMMs (GLIMMIX
260 module, Normal distribution), comparing 11 different candidate models (see electronic appendix, Table 2). To analyse for parental mobbing investment we tested how the number of mobbing calls
262 was affected by treatment, breeding attempt number, and ground vegetation cover using a GLMM (GLIMMIX module, Normal distribution), comparing 14 different candidate models (see electronic
264 appendix, Table 3).

266 **Results**

The number of feeding visits during the pre-exposure period of baseline behaviour did not differ
268 across exposure periods (Fig. 2; Table 1; all pairwise contrasts $p > 0.5$), but increased from first to second breeding attempts (baseline behaviour feeding rate per 45 min (LS means ± SE): first attempt
270 3.8 ± 0.8 vs. second attempt 7.1 ± 0.7; p = 0.05; Fig. 2). Moreover, parents significantly decreased

their number of feeding visits in the presence of a predator model, independent of the type of predator, compared to the control or the period of pre-exposure period of baseline behaviour (interaction treatment × exposure period; Table 1). The response to the predator model, however, depended on breeding attempt number. While parents feeding first broods reacted similarly to all three models (Fig. 2), parents feeding second broods significantly reduced feeding rates when exposed to a predator model (Fig. 2). Parents feeding a second brood showed a stronger feeding rate decrease from the pre-exposure to the model exposure period than parents feeding a first brood (Δ feeding rate pre-/model exposure per 45 min (LS means ± SE): 1^{st} broods 1.6 ± 0.8, $p = 0.02$; 2^{nd} broods 5.2 ± 0.7, $p = <0.0001$).

The approach distance of parents to the model species depended on both breeding attempt number and treatment (Table 2). Parents stayed further away from all models during a first breeding attempt compared to second breeding attempt (LS means ± SE: 1^{st} broods 5.8 ± 1.6 m; 2^{nd} broods 2.5 ± 1.6 m, $p = 0.02$; Table 2). During first breeding attempts parents particularly stayed further away from the predator of adults (sparrowhawk) (Fig. 3), but during the second breeding attempt, parents approached the control species (woodswallow) much closer than the predator of adults and the brood predator (currawong) (Fig. 3).

Predator mobbing intensity depended on treatment, but not on breeding attempt number (Table 3). Parents gave most mobbing calls towards the predator of adults but also mobbed the brood predator (number of mobbing calls per 45 min (LS means ± SE): sparrowhawk 222.2 ± 28.1 vs. currawong 151.9 ± 36.6, $p = 0.03$; sparrowhawk 222.2 ± 28.1 vs. woodswallow 40.8 ± 7.7, $p = <0.0001$; currawong 151.9 ± 36.6 vs. woodswallow 40.1 ± 7.7, $p = 0.002$). The number of mobbing calls parents gave during the presentation of the woodswallow and during the pre-exposure period of baseline behaviour did not differ, verifying that the woodswallow acted as a control (number of calls per 45 min (LS means ± SE): woodswallow 40.8 ± 7.7 vs. baseline behaviour 28.3 ± 3.5, $p = 0.7$).

Discussion

When exposed to predators, parents with dependent offspring have to balance the risk to themselves against the risk to their brood depending on who is at risk. Our study shows that parents in a long-lived bird species shift their risk sensitivity in relation to within-season renesting opportunities. Parents reduced their feeding investment in the presence of a brood predator and a predator of adults but increased their risk sensitivity during second breeding attempts, leading to lower feeding rates in the presence of predators but closer predator approach distances. Nevertheless, mobbing investment was highest towards the predator of adults, independent of breeding attempt number. These results suggest that parental antipredator investment in a long-lived species may change over a breeding season independently of food availability towards being more sensitive to risks threatening offspring survival (Fig. 1 scenario iii, Fig. 3).

Individual plasticity or individual differences?

An important question for the interpretation of our findings is whether the response of the breeding pairs reflects individual plasticity (Martin, 2004) or phenotypic differences between individuals (i.e. personality; Hollander et al., 2008). Under the scenario that personality affects nest predation risk, individuals would show similar risk sensitivity between breeding attempts. Accordingly, bolder and less careful birds would be more likely to have their nests depredated, as thornbills cannot defend their nest against any nest predator species. However, birds that failed in their first breeding attempt were more risk sensitive during their second attempt, and thus it seems unlikely that the observed differences in risk sensitivity reflect personality. Moreover, if personality would affect nest predation risk, natural selection would strongly favour the more successful strategy and eventually eliminate the less successful strategy (Lima, 2009). Finding a link between personality and nest predation risk would be intriguing, but such an effect has not been reported by any study so far. A study in great tits *Parus major* found a link between personality and nest defence (Hollander et al., 2008), but nest defence was not linked to nesting success. Thus, even though we did not test the same individuals

across years and different previous nest predation experiences, the responses we observed are likely to reflect individual plasticity.

Scope of parental antipredation strategies

Parents can be sensitive to variation in nest predation risk and can avoid feeding young in the presence of a brood predator to reduce the risk of exposing their offspring, or to minimise their own risk in the presence of a predator of adults (Eggers et al., 2005, Eggers et al., 2008, Ghalambor & Martin, 2001). Brown thornbill parents reduced their feeding rates in the presence of both predators, which suggests that parents try to maximise both their own and their broods' survival. However, lower provisioning rates in the presence of a predator may negatively influence offspring quality (Martin et al., 2011, Metcalfe & Monaghan, 2001). Nonetheless, limiting the number of feeding visits by breeding individuals has been shown to increase brood survival (Raihani et al., 2010).

Reduced feeding rates in the presence of predators could also be a consequence of parents engaging in other antipredator behaviours. Indeed, during our experiments brown thornbill parents approached and mobbed the predator models instead of feeding their young frequently. Parents generally kept an equal distance from both predator types but gave more mobbing calls towards the predator of adults. While approaching predators can accrue costs (Dugatkin & Godin, 1992), this behaviour may provide direct survival benefits by reducing the probability of future attacks (Godin & Davis, 1995, Pavey & Smyth, 1998). Moreover, mobbing can attract other species to join the mobbing chorus and increase the chance of deterring a predator (Caro, 2005, Krams et al., 2009), which also was the case in a few of our experiments (Schneider & Griesser, 2014). However, predator mobbing near the nest can increase nest predation, as other predators can locate the nest by eavesdropping on mobbing calls (Krama & Krams, 2005, Krams et al., 2007). Thus, it can be suspected that the high mobbing intensity of brown thornbills reflects parental self-defence and thus a prioritisation of adult survival.

Within season change of parental investment

346 Reproductive investment and brood defence may depend on the likelihood of parents producing a second brood, and both of these measures have been shown to increase over the course of a
348 breeding season as a consequence of limited future breeding attempts (Pavel & Bures, 2008, Thorogood et al., 2011, Andersson et al., 1980). Such a within-season change in parental investment
350 has been shown in several short-lived species (Grüebler & Naef-Daenzer, 2008, Verhulst et al., 1997). To our knowledge, our study is the first to show a within-season increase in parental investment in a
352 long-lived species. When confronted with a predator close to their nest, brown thornbill parents increased their investment into offspring survival from first to second breeding attempts, and almost
354 ceased feeding during second breeding attempts. This change in risk sensitivity is unlikely to reflect within-season differences in food availability (see above) or nest predation rates (nest predation
356 rate: 1st attempt: N = 28 out of 50 nests failed, 2nd attempt: N = 14 out of 26 nests failed; Fisher exact test p = 0.99). A likely mechanism for the observed increase in parental risk sensitivity could be that
358 species perceiving a higher ambient predation risk are more risk sensitive and reduce provisioning rates more strongly to reduce brood predation impacts (Ghalambor et al., 2013). As thornbill pairs
360 with a second breeding attempt had already lost their first brood through predation, these pairs experience a higher perceived predation risk and be more sensitive towards predation stimuli, as it is
362 predicted for individuals using Bayesian updating (Schmidt & Whelan, 2010). Short-lived Brewer's sparrow parents who lost their first nest through predation reduced their activity around the nest
364 (Chalfoun & Martin, 2010), but also laid smaller replacement clutches (Chalfoun & Martin, 2010). Brown thornbills, however, tended to increase clutch size during second breeding attempts, with
366 clutches with 4 eggs only being observed during second breeding attempts (based on all nests with clutch size data: first broods N = 28, no nests with clutch size 4; second broods 5 out of 29 broods
368 had a clutch size of 4; Fisher's exact test: p = 0.051). Since clutch size within species is known to decrease with higher predation risk (Martin et al., 2000, Ferretti et al., 2005, Eggers et al., 2006), an
370 increase in clutch size therefore represents a larger reproductive investment by females, particularly so in long-lived species (Fontaine & Martin, 2006, Martin et al., 2006). Thus, brown thornbills

increased both their reproductive investment and antipredator investment during their second breeding attempt. Yet, longitudinal data would be needed to consolidate this species' tendency of increased clutch size investment for later within-season breeding attempts.

Conclusions

Brown thornbills increase their reproductive investment over the course of a breeding season while at the same time becoming more risk sensitive. An increase in risk sensitivity is in line with the idea that individuals use Bayesian updating to adjust their reproductive investment based on the information of prior nest predation events (Schmidt & Whelan, 2010) (Fig. 1, scenario i). However, contrary to earlier studies, an increased risk leads to an increased reproductive investment (Fig. 1, scenario iii). Our data suggest that Bayesian updating can be adopted by species independently of their life-history. While becoming more risk sensitive, brown thornbill parents increased their investment and exposed themselves to greater risk during later breeding attempts, both with respect to predator approach distances and increased clutch size. Although such a pattern may reflect within-season changes in food availability or nest predation risk, these factors remained constant over the breeding season in our study. Thus, a seasonal increase in parental investment could be an adaptive strategy to raise the chance of successful reproduction independently of a species' life-history strategy, yet more studies in other long-lived species are needed to evaluate this hypothesis.

Acknowledgements

We thank Cathrine Young, Naoko Takeuchi and Costantino Marullo for help in the field, Erik Wapstra for his general support, Parks Tasmania for being able to use Trevallyn Nature Recreation Area as a study site, and Western Australian Museum and Tasmanian Museum & Art Gallery for loaning of the models. Matthew Low, Grzegorz Mikusinski, Andy Radford, Simone Webber and anonymous reviewers gave valuable comments on the manuscript. This work was supported by the Swedish Research Council VR (grant no. 621-2008-5349 to MG) and Stiftelsen Lars Hiertas Minne (grant no. FO2010-0041 to NAS).

Tables

Table 1. Results of the GLMM on parental feeding rate in the 45 min per-exposure (baseline behaviour) and model exposure period. $\Delta AIC_C = 6.2$ to second best candidate model, $\omega_i = 0.92$.

effect	n.d.f.	d.d.f.	F-value	p-value
Treatment (predator/control model)	2	38	15	0.23
exposure period (baseline behaviour/ model exposure)	1	59	58.7	<0.0001
breeding attempt number	1	18.8	4.4	0.05
treatment × exposure period	2	59	5.6	0.006
treatment × breeding attempt	2	38	0.9	0.42
exposure period × breeding attempt	1	59	16.2	0.0002

Interaction treatment × exposure period	estimate	SE	d.f.	t-value	p-value
baseline behaviour vs. model exposure					
currawong vs. currawong	5.7 vs. 1.2	0.76	59	5.9	<0.0001
sparrowhawk vs. sparrowhawk	5.6 vs. 1.2	0.76	59	5.8	<0.0001
woodswallow vs. woodswallow	5.1 vs. 3.7	0.76	59	1.8	0.07
model exposure vs. model exposure					
currawong vs. sparrowhawk	1.2 vs. 1.2	0.85	81.5	-0.08	0.93
currawong vs. woodswallow	1.2 vs. 3.7	0.85	81.5	-3.0	0.003
sparrowhawk vs. woodswallow	1.2 vs. 3.7	0.85	81.5	-2.9	0.004

ΔAICc = difference in AICc relative to the best model; ω_i = ΔAICc weight of the model; n.d.f. nominator degrees of freedom, d.d.f. denominator degrees of freedom.

404 **Table 2.** Approach distance of parental birds to the presented model treatments. $\Delta AIC_C = 3.8$ to second best candidate model, $\omega_i = 0.87$.

effect	n.d.f.	d.d.f.	F-value	p-value
treatment	2	38	5.4	0.008
breeding attempt number	1	18.6	5.9	0.02
treatment × breeding attempt	2	38	3.3	0.04

406 ΔAICc = difference in AICc relative to the best model; ω_i = ΔAICc weight of the model; n.d.f. nominator degrees of freedom, d.d.f. denominator degrees of freedom.

Table 3. Number of mobbing calls given by parents to the presented model treatments. $\Delta AIC_C = 4.9$ to second best candidate model, $\omega_i = 0.92$.

effect	n.d.f.	d.d.f.	F-value	p-value
treatment	3	53.2	7.2	0.0004
breeding attempt number	1	16.9	1.2	0.29
vegetation ground cover	1	16.9	1.4	0.26
treatment × breeding attempt	3	53.3	0.3	0.80
treatment × ground cover	3	53.2	2.2	0.10
breeding attempt × ground cover	1	16.9	2.1	0.16

ΔAICc = difference in AICc relative to the best model; ω_i = ΔAICc weight of the model; n.d.f. nominator degrees of freedom, d.d.f. denominator degrees of freedom.

412 **Figure Legends**

Figure 1. Different scenarios of the change of parental investment over a breeding season between
414 first and consecutive breeding attempts: (i) Investment of consecutive brood based on prior nest predation (so called Bayesian updating; Schmidt & Whelan, 2010), will lead to a reduction of the
416 investment. The same response is predicted for individuals in a long-lived species that prioritize future reproductive investment over the one of the current season (Ghalambor & Martin, 2001). (ii)
418 Parents adjust the reproductive investment at the beginning of the breeding season and do not adjust investment in consecutive breeding attempts depending on earlier reproductive success or
420 failure. (iii) Response observed in short-lived species that increase their reproductive investment in consecutive breeding attempts as their scope is to maximise offspring production (Andersson et al.,
422 1980).

424 **Figure 2.** Number of feeding visits (mean±SE) in the 45 min pre-exposure (baseline behaviour) and model exposure periods in relation to breeding attempt number (1^{st} attempt N = 8, 2^{nd} attempt N =
426 13).

428 **Figure 3.** Minimal approach distance (mean±SE) of parental birds to the models dependent on breeding attempt number (1^{st} attempt N = 8, 2^{nd} attempt N = 13). Letters above bars (a, b, c) indicate
430 statistically significant differences.

References

Andersson, M., Wiklund, C. G. & Rundgren, H. 1980. Parental defense of offspring - A model and an example. *Animal Behaviour* **28**: 536-542.

Barker, R. & Vestjens, W. 1989. *Food of Australian Birds 1. Non-passerines*. CSIRO Publishing.

Barker, R. & Vestjens, W. 1990. *Food of Australian Birds 2. Passerines*. CSIRO Publishing.

Bureau of Meteorology (2013) Climate Data Online. pp. Australian Government, http://www.bom.gov.au/climate/data/.

Burnham, K. P. & Anderson, D. R. 2002. *Model selection and multimodel interference: a preactical information-theoretic approach,* 2nd ed. Springer Science + Business Media, New York.

Caro, T. M. 2005. *Antipredator defences in birds and mammals*. The University of Chicago Press, Chicago.

Chalfoun, A. D. & Martin, T. E. 2010. Parental investment decisions in response to ambinet nest-predation risk versus actual predation on the the prior nest. *Condor* **112**: 701-710.

Charlesworth, B. 1980. *Evolution in age-structured populations*. Cambridge University Press, Cambridge and New York.

Dugatkin, L. A. & Godin, J. G. J. 1992. Prey Approaching Predators - a Cost-Benefit Perspective. *Annales Zoologici Fennici* **29**: 233-252.

Eggers, S., Griesser, M. & Ekman, J. 2005. Predator-induced plasticity in nest visitation rates in the Siberian jay (Perisoreus infaustus). *Behavioral Ecology* **16**: 309-315.

Eggers, S., Griesser, M. & Ekman, J. 2008. Predator-induced reductions in nest visitation rates are modified by forest cover and food availability. *Behavioral Ecology* **19**: 1056-1062.

Eggers, S., Griesser, M., Nystrand, M. & Ekman, J. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. *Proceedings of the Royal Society B-Biological Sciences* **273**: 701-706.

Emmering, Q. C. & Schmidt, K. A. 2011. Nesting songbirds assess spatial heterogeneity of predatory chipmunks by eavesdropping on their vocalizations. *Journal of Animal Ecology* **80**: 1305-1312.

Ferretti, V., Llambias, P. E. & Martin, T. E. 2005. Life-history variation of a neotropical thrush challenges food limitation theory. *Proceedings of the Royal Society B: Biological Sciences* **272**: 769-773.

Fontaine, J. J. & Martin, T. E. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters* **9**: 428-434.

Ghalambor, C. K. & Martin, T. E. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science* **292**: 494-497.

Ghalambor, C. K. & Martin, T. E. 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behavioral Ecology* **13**: 101-108.

Ghalambor, C. K., Peluc, S. I. & Martin, T. E. 2013. Plasticity of parental care under the risk of predation: how much should parents reduce care? *Biology Letters* **9**.

Godin, J. G. J. & Davis, S. A. 1995. Who dares, benefits: Predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. *Proceedings of the Royal Society of London Series B-Biological Sciences* **259**: 193-200.

Green, D. J. & Cockburn, A. 1999. Life history and demography of an uncooperative Australian passerine, the brown thornbill. *Australian Journal of Zoology* **47**: 633-649.

Green, D. J. & Cockburn, A. 2001. Post-fledging care, philopatry and recruitment in brown thornbills. *Journal of Animal Ecology* **70**: 505-514.

Green, D. J., Peters, A. & Cockburn, A. 2002. Extra-pair paternity and mate-guarding behaviour in the brown thornbill. *Australian Journal of Zoology* **50**: 565-580.

Griesser, M., Schneider, N. A., Collis, M.-A., Overs, A., Guppy, M., Guppy, S., Takeuchi, N., Collins, P., Peters, A. & Hall, M. L. 2012. Causes of Ring-Related Leg Injuries in Birds – Evidence and Recommendations from Four Field Studies. *PloS ONE* **7**: e51891.

Grüebler, M. U. & Naef-Daenzer, B. 2008. Postfledging parental effort in barn swallows: evidence for a trade-off in the allocation of time between broods. *Animal Behaviour* **75**: 1877-1884.

Higgins, P. J. & Peter, J. M. (Eds.) (2002) *Handbook of Australian, New Zealand and Antarctic birds. Volume 6: Pradalotes to Shrike-thrushes,* Melbourne, Australia, Oxford University Press.

Higgins, P. J., Peter, J. M. & Cowling, S. J. (Eds.) (2006) *Handbook of Australian, New Zealand and Antarctic birds. Volume 7: Boatbill to Starlings,* Melbourne, Oxford University Press.

Hollander, F. A., Van Overveld, T., Tokka, I. & Matthysen, E. 2008. Personality and Nest Defence in the Great Tit (Parus major). *Ethology* **114**: 405-412.

Krama, T. & Krams, I. 2005. Cost of mobbing call to breeding pied flycatcher, Ficedula hypoleuca. *Behavioral Ecology* **16**: 37-40.

Krams, I., Berzins, A. & Krama, T. 2009. Group effect in nest defence behaviour of breeding pied flycatchers, Ficedula hypoleuca. *Animal Behaviour* **77**: 513-517.

Krams, I., Krama, T., Igaune, K. & Mand, R. 2007. Long-lasting mobbing of the pied flycatcher increases the risk of nest predation. *Behavioral Ecology* **18**: 1082-1084.

Kroodsma, D. E., Byers, B. E., Goodale, E., Johnson, S. & Liu, W. C. 2001. Pseudoreplication in playback experiments, revisited a decade later. *Animal Behaviour* **61**: 1029-1033.

Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews* **84**: 485-513.

Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation - A review and prospectus. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **68**: 619-640.

Low, M., Arlt, D., Eggers, S. & Pärt, T. 2010. Habitat-specific differences in adult survival rates and its links to parental workload and on-nest predation. *Journal of Animal Ecology* **79**: 214-224.

Marchant, S. & Higgins, P. J. (Eds.) (1993) *Handbook of Australian, New Zealand and Antarctic birds. Volume 2: Raptors to lapwings.,* Melbourne, Oxford University Press.

Martin, T. E. 2004. Avian life-history evolution has an eminent past: Does it have a bright future? *Auk* **121**: 289-301.

Martin, T. E., Bassar, R. D., Bassar, S. K., Fontaine, J. J., Lloyd, P., Mathewson, H. A., Niklison, A. M. & Chalfoun, A. 2006. Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. *Evolution* **60**: 390-398.

Martin, T. E. & Briskie, J. V. 2009. Predation on Dependent Offspring A Review of the Consequences for Mean Expression and Phenotypic Plasticity in Avian Life History Traits. *Year in Evolutionary Biology 2009* **1168**: 201-217.

Martin, T. E., Lloyd, P., Bosque, C., Barton, D. C., Biancucci, A. L., Cheng, Y.-R. & Ton, R. 2011. Growth rate variation among passerine species in tropical and temperate sites: An antagonistic interaction between parental food provisioning and nest predation risk. *Evolution* **65**: 1607-1622.

Martin, T. E., Martin, P. R., Olson, C. R., Heidinger, B. J. & Fontaine, J. J. 2000. Parental Care and Clutch Sizes in North and South American Birds. *Science* **287**: 1482-1485.

Metcalfe, N. B. & Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology and Evolution* **15**: 254-260.

Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. Wiley & Sons, Inc., new York.

Pavel, V. & Bures, S. 2008. Nest defence in the meadow pipit Anthus pratensis: the influence of renesting potential. *Journal of Ethology* **26**: 367-373.

Pavey, C. R. & Smyth, A. K. 1998. Effects of avian mobbing on roost use and diet of powerful owls, *Ninox strenua*. *Animal Behaviour* **55**: 313-318.

Quinn, G. P. & Keough, M. J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press.

Raihani, N. J., Nelson-Flower, M. J., Moyes, K., Browning, L. E. & Ridley, A. R. 2010. Synchronous provisioning increases brood survival in cooperatively breeding pied babblers. *Journal of Animal Ecology* **79**: 44-52.

Recher, H. F., Majer, J. D. & Ganesh, S. 1996. Seasonality of canopy invertebrate communities in eucalypt forests of eastern and western Australia. *Australian Journal of Ecology* **21**: 64-80.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* **9**: 1-48.

Roff, D. A. 1992. *The Evolution of Life Histories: Theories and Analysis*. Chapman & Hall, New York.

Russell, E. M. 2000. Avian life histories: Is extended parental care the southern secret? *Emu* **100**: 377-399.

SAS (2006) The GLIMMIX Procedure. pp. SAS Institute Inc, Cary, NC, USA.

Schmidt, K. A. & Whelan, C. J. 2010. Nesting in an uncertain world: information and sampling the future. *Oikos* **119**: 245-253.

Schneider, N. A. & Griesser, M. 2013. Incubating females use dynamic risk assessment to evaluate the risk posed by different predators. *Behavioral Ecology* **24**: 47-52.

Schneider, N. A. & Griesser, M. 2014. The alarm calling system of breeding Brown Thornbills *Acanthiza pusilla* - self-defence or nest defence? *Journal of Ornithology* ***In Press***.

Siikamäki, P. 1998. Limitation of reproductive success by food availability and breeding time in pied flycatchers. *Ecology* **79**: 1789-1796.

Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, London.

Thorogood, R., Ewen, J. G. & Kilner, R. M. 2011. Sense and sensitivity: responsiveness to offspring signals varies with the parent' potential to breed again. *Proceedings of the Royal Society B: Biological Sciences* **278**: 2638-2645.

Valone, T. J. 2006. Are animals capable of Bayesian updating? An empirical review. *Oikos* **112**: 252-259.

Verhulst, S., Tinbergen, J. M. & Daan, S. 1997. Multiple breeding in the Great Tit. A trade-off between successive reproductive attempts? *Functional Ecology* **11**: 714-722.

Wallin, K. 1987. Defence as Parental Care in Tawny Owls (*Strix aluco*). *Behaviour* **102**: 213-230.